

Microbial CH₄ and N₂O consumption in acidic wetlands

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Acidic wetlands are global sources of the atmospheric greenhouse gases methane (CH₄), and nitrous oxide (N₂O). Consumption of both atmospheric gases has been observed in various acidic wetlands, but information on the microbial mechanisms underlying these phenomena is scarce. A substantial amount of CH₄ is consumed in sub soil by aerobic methanotrophs at anoxic–oxic interfaces (e.g., tissues of *Sphagnum* mosses, rhizosphere of vascular plant roots). *Methylocystis*-related species are likely candidates that are involved in the consumption of atmospheric CH₄ in acidic wetlands. Oxygen availability regulates the activity of methanotrophs of acidic wetlands. Other parameters impacting on the methanotroph-mediated CH₄ consumption have not been systematically evaluated. N₂O is produced and consumed by microbial denitrification, thus rendering acidic wetlands as temporary sources or sinks for N₂O. Denitrifier communities in such ecosystems are diverse, and largely uncultured and/or new, and environmental factors that control their consumption activity are unresolved. Analyses of the composition of N₂O reductase genes in acidic wetlands suggest that acid-tolerant Proteobacteria have the potential to mediate N₂O consumption in such soils. Thus, the fragmented current state of knowledge raises open questions concerning methanotrophs and denitrifiers that consume atmospheric CH₄ and N₂O in acidic wetlands.

Keywords: Peat, bog, fen, CH₄ cycle, nitrogen cycle, greenhouse gas sink, soil microbiology

INTRODUCTION

Microbial communities of acidic wetlands are responsible for emissions of the potent greenhouse gases methane (CH₄), and nitrous oxide (N₂O; Conrad, 1996; Whalen, 2005; Denman et al., 2007). The largest single global source of atmospheric CH₄ (100–237 Gt year^{−1}) are acidic wetlands, such as peat bogs and fens that cover 3.5% of the terrestrial surface, but store about 30% of global carbon of terrestrial ecosystems (Gore, 1983; Denman et al., 2007). Largest sources of atmospheric N₂O are soils under natural vegetation and agricultural use; nonetheless, certain acidic wetlands that have a high nitrogen content were recently identified as significant sources of N₂O displaying N₂O emissions in the range of those observed for agricultural soils (Denman et al., 2007; Repo et al., 2009; Marushchak et al., 2011). Conservative estimates suggest that 0.6% of the global annual emission of N₂O might be attributed to such acidic wetlands (Repo et al., 2009).

Acidic wetlands are covered by water-adapted vascular plants, and mosses of the genus *Sphagnum* (Gorham, 1991). Microbes that produce CH₄ are methanogenic Archaea, and those that are the main source of N₂O are denitrifiers in anoxic habitats like wetlands (Conrad, 1996; Ferry, 1999; Drake et al., 2009). CH₄ produced by methanogens is further oxidized by aerobic methanotrophs, which thrive as a significant part of wetland microbial communities and mitigate the net CH₄ flux into the atmosphere (Hanson and Hanson, 1996; Shannon et al., 1996; Whalen, 2005; Knorr et al., 2008; Hornibrook et al., 2009). Atmospheric oxygen may penetrate soil due to water table draw downs, and gas transport through the aerenchyma of vascular plants into the rhizosphere (Moog and Bruggemann, 1998; Kettunen et al., 1999; Mainiero and Kazda,

2005; Paul et al., 2006). Acidic wetlands may temporarily turn into sinks of atmospheric CH₄, or at least have the potential to consume atmospheric CH₄ (≤ 1.75 ppmv; Table 1; Whalen and Reeburgh, 2000; Jauhiainen et al., 2005; Elberling et al., 2011), a fact that is currently underappreciated, and poorly understood on the level of microbial communities.

Association of denitrifiers with N₂O production in nitrogen-rich acidic wetlands is indicated by process-orientated studies of water-logged acidic soils, and denitrification is suggested as the primary N₂O producing process in such systems where the water filled pore space exceeds 70% (Davidson, 1991). Denitrifiers catalyze the sequential reduction of N-oxides to nitrous oxide (N₂O) and/or dinitrogen (N₂) via the sequential action of nitrate, nitrite, nitric oxide, and nitrous oxide reductases (Zumft, 1997). Subunits that contain the catalytic center are encoded by *narG/napA*, *nirK/nirS*, *norB*, and *nosZ*. Dissimilatory reduction of nitrate via nitrite to ammonium (DNRA) might produce N₂O under oxygen limited conditions via the unspecific interaction of nitrite with nitrate reductase (Smith and Zimmermann, 1981; Smith, 1983). However, DNRA potentials are low in acidic wetland soils, and free nitrite is virtually absent from such soils, suggesting that DNRA is negligible with regards to N₂O production (Anderson and Leine, 1986; Bowden, 1987). Significant products of chemodenitrification are NO and NO₂ rather than N₂O (van Cleemput, 1998; Kappelmeier et al., 2003; Kresovic et al., 2009). N₂O is also produced as a by-product during the aerobic conversion of ammonia to nitrate by nitrifiers, but nitrification is the primary source of N₂O in oxic rather than water-logged soils (Davidson, 1991; Conrad, 1996). Despite the importance of denitrifiers for N₂O production

Table 1 | Acidic wetlands exhibiting consumption of atmospheric CH₄ or N₂O, and associated methanotroph and denitrifier communities if such data were available.

Wetland	Methanotrophs	Denitrifiers	Consumption of atmospheric		Reference
			CH ₄	N ₂ O	
Fen (Germany) pH 4.2	<i>Methylocystis</i> , <i>Methylocella</i> (<i>Methylococcus</i>) ^A [<i>pmoA</i> , <i>mmoX</i>] n.a. ^B	Fen clusters one to five [nosZ] (next cultivated relatives: <i>Bradyrhizobium japonicum</i> , <i>Achromobacter xylosoxidans</i> , <i>Azospirillum lipoferum</i> , <i>Azospirillum irakense</i>) n. a.	–5.1 μmol g _{soil} DW ^{–1} h ^{–1}	–19.0 to –105.0 nmol h ^{–1} g _{soil} DW ^{–1}	Wieczorek et al. (2011), Palmer et al. (2010)
Sovetskii raised bog (Russia) pH 3.8–4.2	n. a.	n. a.	–1.0 nmol g _{soil} DW ^{–1} h ^{–1} F	n. a.	Dedysh and Panikov (1997)
Cryoturbated and unturbated tundra peat soil (Russia) pH 3–4	n. a.	11 operational taxonomic units of nosZ (next cultivated relatives: <i>Mesorhizobium</i> sp. D187B, <i>Bradyrhizobium</i> sp. BTAi1, <i>Achromobacter xylosoxidans</i> , <i>Pseudomonas lini</i> , <i>Ralstonia solanacearum</i>) n. a.	n. a.	–9.4 to –56.8 nmol m ^{–2} h ^{–1}	Palmer et al. (2011), Marushchak et al. (2011)
Peat swamp forest (Indonesia) pH 3.3	n. a.	n. a.	–6.3 μmol m ^{–2} h ^{–1} D	n. a.	Jauhainen et al. (2005)
Boreal Wetland (Alaska, USA) pH < 4.0	n. a.	n. a.	–2.3 μmol m ^{–2} h ^{–1} D	n. a.	Whalen and Reeburgh (2000)
Boreal Fens (Finland) pH < 4.5	n. a.	n. a.	–0.2 nmol g _{soil} DW ^{–1} h ^{–1} E	n. a.	Kettunen et al. (1999)
Tropical peatland (Kalimantan, Indonesia) pH 3–4	n. a.	n. a.	n. c. ^C	–0.3 to –1.0 μmol m ^{–2} h ^{–1} D	Inubushi et al. (2003)
Neleger forest–alas ecosystem (Russia) pH 6.3	n. a.	n. a.	–1 to –0.3 mmol m ^{–2} h ^{–1}	–0.1 to –1.7 μmol m ^{–2} h ^{–1}	Takakai et al. (2008)

^ATaxon with little abundance (<5%).^Bn. a., Not analyzed.^Cn. c., No consumption.^DCalculated based on values of the respective study.^ECalculated based on reported first order rate constant (i.e., $-0.03 \text{ h}^{-1} \text{ g}_{\text{soil DW}}^{-1}$) at 1.8 ppmv (Assumption: water content 50%, $1.8 \text{ ppmv} = 2.5 \text{ nM}$; thus, dissolved CH₄ concentration is $5 \text{ pmol g}_{\text{soil DW}}^{-1}$).^FThis rates are calculated from first order rate constants of CH₄ consumption (i.e., based on K_{CH_4} [43 nM; or $\sim 3.6 \text{ nmol g}_{\text{soil wet weight}}^{-1}$] and V_{max} [38.5 nmol g_{soil wet weight}^{–1}] values as reported in the reference) at a headspace concentration of 1.8 ppmv. The water content was about 95%.

in water-logged soils and the wealth of information on denitrifiers of agricultural and pH-neutral upland soils, studies addressing acid-tolerant denitrifiers in acidic wetlands are just emerging and under-represented in current literature. Evidence is accumulating that soils including acidic wetlands can act as temporary sinks for N₂O (Inubushi et al., 2003; Hadi et al., 2005; Chapuis-Lardy et al., 2007; Goldberg et al., 2010). Indeed, negative fluxes of up to $-1.7 \mu\text{mol N}_2\text{O m}^{-2} \text{h}^{-1}$ were observed *in situ* for acidic wetlands (Table 1). Thus, the review intends to delineate the current understanding of microbial communities in acidic wetlands for CH₄ and N₂O consumption and to highlight research needs.

METHANOTROPHS OF ACIDIC WETLANDS

CH₄ fluxes of acidic wetlands are highly variable due to non-linear interactions of environmental factors that control methanogenesis, methanotrophy, and CH₄ gas transport (Whalen, 2005; Spahn et al., 2011). One reason of high spatial and temporal variability of CH₄ exchange with the atmosphere might be a mitigation of net flux by consumption of atmospheric CH₄ (Wieczorek et al., 2011). Hot spots of activity of methanotrophs in acidic wetlands are anoxic–oxic interfaces, where CH₄ and oxygen gradients overlap (Sundh et al., 1995; Kettunen et al., 1999). Thus changes in oxygen availability alter both CH₄ consumption, and production, and hence, reduce or increase net flux of CH₄ from soil into the atmosphere (Kettunen et al., 1999; Whalen, 2005).

Prevalent methanotrophs of acidic wetlands belong to Alphaproteobacteria (Chen et al., 2008a; Dedysh, 2009; Wieczorek et al., 2011). Total cell numbers of methanotrophs of acidic wetlands range from 10⁶ to 10⁸ cells per gram of wet weight (Sundh et al., 1995; Dedysh et al., 2001, 2003; Dedysh, 2002, 2009; Belova et al., 2011). Methanotrophic pure cultures have primarily been isolated from *Sphagnum*-covered wetlands, and are acid-tolerant strains of *Methylocystis* (Methylocystaceae), *Methylocella*, and *Methylocapsa* (both Beijerinckiaceae; Dedysh et al., 2001, 2003; Dedysh, 2002, 2009; Kip et al., 2011). *Methylocella* species, and some species of *Methylocystis* and *Methylocapsa* utilize also simple multicarbon compounds, such as acetate (Dedysh et al., 2005; Theisen et al., 2005; Dunfield et al., 2010; Belova et al., 2011). Fluctuations of soil-internal methanogenesis may be caused by varying exudation of plants and redox conditions due to water table changes that can be consequences of drought periods, or heavy rainfall (Knorr et al., 2008; Knorr and Blodau, 2009; Dorodnikov et al., 2011). Acetate-utilizing methanotrophs are largely independent of such CH₄ deficits in acidic wetlands.

Methylocystis strain H2s apparently represents a key methanotroph in acidic wetlands (Belova et al., 2011; Wieczorek et al., 2011). Strain H2s-related 16S rRNA genes ubiquitously occur in northern wetlands, and contribute with 18–58% (i.e., 0.4×10^7 to 3.4×10^7 cells g⁻¹ of wet weight) to the alphaproteobacterial methanotrophs in such wetlands (Belova et al., 2011). Uncultivated species that are phylogenetically related to *Methylocystis*, and *Methylocapsa* are associated with hyaline cells of submerged mosses of *Sphagnum*. These *Sphagnum* methanotroph associations have been found in various northern wetlands (Kip et al., 2010). Methanotrophs apparently contribute up to 30% to carbon assimilation of the moss (Raghoebarsing et al., 2005; Kip et al., 2010; Larmola et al., 2010; Parmentier et al., 2011). The

association is, based on current observations, not specific since different methanotroph-free *Sphagnum* species can be colonized by methanotrophs that were provided from the same *Sphagnum* individual (Larmola et al., 2010). The physiological basis of the interaction between methanotroph and moss has not been fully resolved.

Wetland methanotroph communities are usually dominated by Alphaproteobacteria, but gammaproteobacterial methanotrophs may also be present (Morris et al., 2002; Chen et al., 2008a,b; Wieczorek et al., 2011). Some of them (*Methylobacter*-, *Methylosoma*-related strains) have been isolated, which represent the first acid-tolerant members of the Methylococcaceae (Kip et al., 2011). All cultured methanotrophs of acidic wetlands are acid-tolerant and have growth optima below pH6 (Dedysh, 2009; Kip et al., 2011). Most information on the identities and physiologies of methanotrophs of acidic wetlands are derived from *Sphagnum*-associated microbial communities, but there is a lack of information on vascular plant-associated methanotrophs in acidic wetlands.

SPECIALIZED METHANOTROPHS MEDIATE CH₄ SINK ACTIVITY OF ACIDIC WETLANDS

Acidic wetlands may temporally turn into net sinks of atmospheric CH₄, which has been documented in various studies, or have the capability to utilize atmospheric CH₄ concentrations (Table 1; Figure 1; Dedysh and Panikov, 1997; Kettunen et al., 1999; Whalen and Reeburgh, 2000; Jauhiainen et al., 2005; Elberling et al., 2011; Wieczorek et al., 2011). Many wetland sites have annual emission rates of less than 3.8 mol CH₄ ha⁻² year⁻¹ (Dalal and Allen, 2008) indicating not necessarily only low CH₄ production, but also a certain proportion of consumption of atmospheric CH₄ over the year.

A very limited number of studies analyzed the composition of methanotroph communities of acidic wetlands, and measured the potential of the respective wetland to consume atmospheric CH₄ (Table 1). *Methylocystis* species that were frequently detected in acidic wetlands are closely related to the solely known methanotroph strains that are capable of consumption of atmospheric CH₄, i.e., strains LR1, SC2, and DWT (Dunfield et al., 1999, 2002; Kolb et al., 2005; Baani and Liesack, 2008; Dedysh, 2009; Wieczorek et al., 2011). Nonetheless, *pmoA2* genes (that encode for the hydroxylase subunit of a high affinity CH₄ mono-oxygenase) that would indicate the capability of consumption of atmospheric CH₄ (Dunfield et al., 2002; Yimga et al., 2003; Ricke et al., 2004; Baani and Liesack, 2008) have only been detected at low relative abundances (<5%; Wieczorek et al., 2011). To warrant consumption of atmospheric CH₄ in wetlands a small fraction (about 10⁷ cells per gram dry weight in forest soils that consume atmospheric CH₄; Kolb et al., 2005; Degelmann et al., 2010) of the total cell number of present methanotrophs (about 10⁸ cells per gram dry weight) need presumably be active to allow for consumption of atmospheric CH₄ at rates that were observed in acidic wetland sites. The major proportion of detectable *pmoA* (encodes the beta-subunit of a low affinity membrane bound CH₄ mono-oxygenase) and *mmoX* (encodes the hydroxylase subunit of a low affinity cytoplasmic bound CH₄ mono-oxygenase) genes in an acidic wetland soil that exhibited the capability of consumption of atmospheric levels

of CH₄ (i.e., 82 and 64%, respectively), affiliated with genes of *Methylocystis* (Wieczorek et al., 2011). Some *Methylocystis* species have the capability to utilize atmospheric CH₄ concentrations. The abundant *Methylocystis* strain H2s harbors as well *pmoA2* indicating that this methanotroph may consume atmospheric CH₄ (Dedysh, personal communication). Thus, *Methylocystis* species of acidic wetlands likely are capable of atmospheric CH₄ consumption (Figure 1), and may have the advantage to survive more likely periods of CH₄ deficiency, may be periodically the case in minerotrophic fens, and at oxygen-saturated surface-near soil layers.

Recently described thermoacidophilic methanotrophs of the *Methylacidiphilaceae* (Op den Camp et al., 2009) as well as anaerobic methanotrophs *Candidatus* “Methyloirabilis oxyfera” (Ettwig et al., 2010) have not been detected in acidic wetlands.

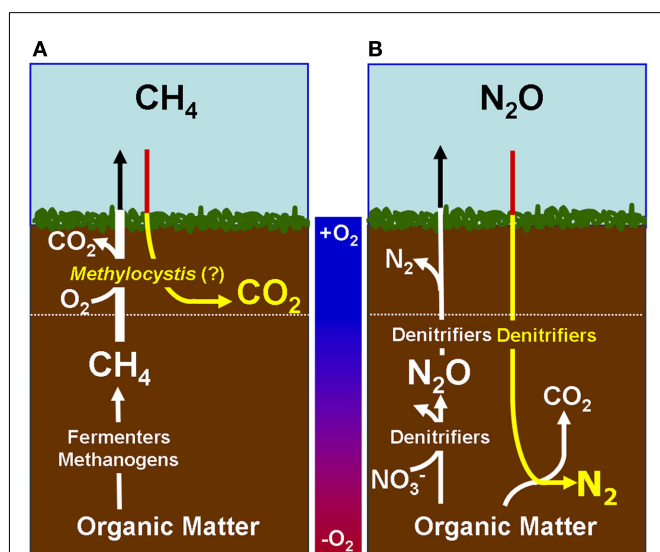


FIGURE 1 | Proposed Model of Microbes that are responsible of atmospheric sink function of CH₄ and N₂O in natural wetlands. The quantitative contribution to global net fluxes of CH₄ and N₂O into the atmosphere has not been evaluated in acidic wetlands. **(A)** Acidic wetland covered by *Sphagnum* plants with low nitrogen input and mineralization rates. White Pathway: Plant-derived organic matter is degraded by microbial fermentation, acetogenesis, and methanogenesis to CH₄ that is transported to oxygen-saturated zones close to the surface. The thickness of the oxygen-saturated layer is dependent of water table level (white dotted line). Methanotrophs (such as *Methylocystaceae*, *Beijerinckiaceae*, but as well *Methylococcaceae*) consume up to 90% of methanogenic CH₄. Products are microbial biomass and CO₂. The not-consumed proportion of CH₄ is released into the atmosphere. Methanotrophs convert CH₄ to carbon dioxide (CO₂) which is released into the atmosphere. Yellow pathway: *Methylocystis* species likely consume atmospheric CH₄ when CH₄ supply from anoxic zones is limited. **(B)** Natural wetland with high nitrogen input and mineralization rates (e.g., minerotrophic fens, Palsa peats). White pathway: In nitrogen-rich acidic wetlands (e.g., Palsa peats) a part of anaerobic organic matter degradation intermediates are consumed by denitrifiers that reduce NO₃⁻ to N₂O and N₂. N₂O and N₂ is released into the atmosphere. Ammonia-oxidizing bacteria (AOB) are known to produce small amounts of N₂O during oxidation of ammonia (Schmidt et al., 2004; Braker and Conrad, 2011). Yellow pathway: Under as-yet unresolved environmental conditions atmospheric N₂O may be further reduced to N₂ by to date not cultured denitrifiers that use electrons from organic matter.

In summary, *Methylocystis* are likely involved for consumption of atmospheric CH₄ in acidic wetlands. Nonetheless, an unequivocal experimental proof is missing. The role of other methanotrophs in acidic wetlands (i.e., *Beijerinckiaceae*, and *Methylococcaceae*) in consumption of atmospheric CH₄ is not fully unresolved, but not very likely based on their low affinities for CH₄. It is not likely that “*M. oxyfera*” is involved in N₂O cycling since it lacks nitric oxide reductase.

DO DENITRIFIERS CONSUME N₂O IN ACIDIC WETLANDS?

One of the most remarkable features of denitrifiers is their capacity to produce and consume N₂O (Table 1; Figure 1; Zumft, 1997). Such organisms are widely distributed in various environments and highly diverse (e.g., Zumft, 1997; Braker and Conrad, 2011). Not all denitrifiers known to date are capable of N₂O consumption (Zumft and Kroneck, 2007). However, N₂O is a common intermediate during denitrification and serves as sole electron acceptor for supporting growth of many denitrifiers (Zumft, 1997; Strohm et al., 2007). DNA based stable isotope probing with ¹³C-labeled succinate as electron donor and N₂O as electron acceptor and cultivation-based studies demonstrated growth of putative denitrifiers by N₂O reduction in rice field soil (Ishii et al., 2011). These findings are in line with a ΔG° of N₂O reduction to N₂ that approximates −340 kJ mol^{−1} under standard conditions, indicating a highly exergonic process (Zumft and Kroneck, 2007). Thus, it might not be surprising that N₂O consumption by soil communities is a more common phenomenon than previously thought (Table 1; reviewed in Holtan-Hartwig et al., 2000; Chapuis-Lardy et al., 2007).

N₂O reductases of denitrifiers catalyze the efficient reduction of N₂O to N₂ and are copper-dependent metallo-enzymes that exhibit K_M values in the lower micromolar range for N₂O, highlighting the potential of denitrifiers to consume low concentrations of N₂O (Zumft, 1997). Abiotic conversion of N₂O at ambient temperatures might occur with (reduced) transition-metal complexes (which occur in the active site of N₂O converting enzymes) and metal amides (Banks et al., 1968; Zumft and Kroneck, 2007). Metallo-enzymes like carbon monoxide dehydrogenase and cobalamin-dependent methionine synthase are also capable of reducing N₂O to N₂, while nitrogenase converts N₂O to NH₃; bacterial nitrite cytochrome c reductase transforms N₂O to an unknown product (Jensen and Burris, 1986; Bannerjee and Matthews, 1990; Lu and Ragsdale, 1991; Drummond and Matthews, 1994; Stach et al., 2000). Such enzymes are hosted by diverse organisms including non-denitrifiers (see references in Zumft, 1997; Zumft and Kroneck, 2007). However, the conversion of N₂O by these aforementioned enzymes is regarded as a non-physiological reaction. Low K_M values and high specific activities for N₂O (as were demonstrated for N₂O reductases of denitrifiers) have not been demonstrated for such enzymes, suggesting a minor role, if any, for the consumption of atmospheric N₂O concentrations (319 ppb, equivalent to app. 8 nmol N₂O per liter soil solution; Conrad, 1996) in soils (Zumft, 1997; Stach et al., 2000; Zumft and Kroneck, 2007). In this context, dissimilatory reducers of nitrate producing ammonia of the *Enterobacteriaceae* that were shown to consume N₂O in the laboratory displayed a K_M value of 3 mM for N₂O, likewise suggesting that the N₂O reduction is

a non-physiological reaction and probably of minor importance *in situ* (Kaldorf et al., 1993). Moreover, assimilatory reduction of N₂O that might theoretically proceed via nitrogenase action was not detected in soils (Vieten et al., 2008). Thus, denitrifiers hosting N₂O reductases deserve primary attention in the context of N₂O consumption in soils.

Denitrification rates and the ratio of N₂O to total nitrogen gas products are regulated by oxygen availability, pH, temperature, carbon to nitrogen ratio, the availability of substrates, and electron acceptors, as well as by the denitrifier community composition (van Cleemput, 1998; Dörsch et al., 2011). Anoxia (as indicated by a water filled pore space of greater than 60%), a carbon to nitrogen ratio greater than 30, and pH-neutral conditions favor complete denitrification to N₂ in soils including acidic wetlands (Conrad, 1995, 1996; Klemetsson et al., 2005; Cuhel et al., 2010; Braker and Conrad, 2011). A pH value below 5 is often encountered in peatlands, and is hypothesized to impair N₂O reduction and to increase the product ratio of N₂O to N₂ (Simek and Cooper, 2002; Cuhel et al., 2010). However, acidic wetlands host acid-tolerant denitrifiers capable of N₂O reduction and complete denitrification (Palmer et al., 2010, 2011). Moreover, evidence of active denitrification-associated N₂O production and consumption, (including consumption of atmospheric N₂O concentrations) was obtained by compound specific stable isotope analyses of N₂O in one acidic wetland (Goldberg et al., 2008, 2010). In that specific wetland, $\delta^{15}\text{N}$ values indicated that N₂O produced in deep soil layers was partially consumed upon its diffusion to the soil surface (Goldberg et al., 2008, 2010), suggesting that denitrifiers might contribute to the mitigation of N₂O emission from acidic wetlands. Denitrifiers that exhibit the genetic potential to consume N₂O were detected in acidic wetlands by the analysis of *nosZ* genes. Detected *nosZ* genes in acidic wetlands mostly affiliated with *nosZ* from uncultured soil bacteria or were only distantly related to known genes, suggesting a wealth of uncultured denitrifier diversity in acidic wetlands (Palmer et al., 2010, 2011). Phylogenies of *nosZ* and 16S rRNA genes from the same organisms are basically congruent (Jones et al., 2008; Palmer et al., 2009), allowing to speculate on the identity of organisms hosting the detected *nosZ*. Thus, putative N₂O reducers in acidic wetlands include Alphaproteobacteria (*Azospirillum*, *Brady*-, and

Mesorhizobium), Betaproteobacteria (*Achromobacter*, *Ralstonia*), and Gammaproteobacteria (*Pseudomonas*). However, it remains to be determined whether the detected N₂O reductase genes were expressed, i.e., the detected organisms reduce N₂O *in situ* (Figure 1).

Analyses of other genes associated with denitrification corroborate that acidic wetlands harbor diverse and new denitrifiers (Palmer et al., 2010, 2011). However, given the low number of studies addressing N₂O-consuming denitrifier communities in acidic wetlands, and the selectivity of PCR-based gene marker analyses, the present studies have to be regarded as providing a minimal estimate of denitrifier diversity capable of N₂O consumption (Throback et al., 2004; Green et al., 2010; Heylen et al., 2011; Jones et al., 2011). The fact that high affinity respiratory N₂O reduction occurs in non-denitrifying organisms that reduce nitrate but lack nitrite reductase activity, and that nitrifiers were shown to have the capability to consume N₂O and produce N₂ further complicates matters (Yoshinari, 1980; McEwan et al., 1985; Zumft, 1997; Schmidt et al., 2004). Nevertheless, the relevance of N₂O consumption for mitigation of N₂O emissions, and eventually a temporary sink function of acidic wetlands for N₂O is emerging, although the physiology and taxonomic identity of “microbial catalysts” have not been sufficiently resolved. Furthermore, the regulation of N₂O reduction *in situ* and on cellular level, and thus the potential of the soil to reduce N₂O to N₂, and the diffusivity of N₂O within the soil profile will impact the sink functions of wetland soils for N₂O but are likewise only poorly resolved.

FUTURE PERSPECTIVES

Few studies addressed the role of methanotrophs and denitrifiers in consumption of atmospheric CH₄ and N₂O in acidic wetlands. Potential consumption activities have been measured in laboratory-scale experiments, and first evidence for denitrification-associated N₂O consumption *in situ* is available. Systematic *in situ* flux measurements combined with measurements of environmental parameters, consumption potentials, stable isotope signatures of carbon and nitrogen in CH₄ and N₂O pools, and community analyses are needed to improve our understanding of environmental factors that trigger CH₄ and N₂O consumption in acidic wetland soils.

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